

## REFLECTIONS ON A LIFETIME OF ORNITHOLOGICAL RESEARCH The 2000 Margaret Morse Nice Lecture

SUSAN M. SMITH<sup>1</sup>

I still remember my excitement when, as a beginning graduate student, I first discovered the work by Margaret Morse Nice on Song Sparrows (*Melospiza melodia*). Her brilliant field research on color-banded Song Sparrows (Nice 1937, 1943) remains the standard of excellence for avian studies to this day. Certainly her work has continued to inspire me throughout my professional life. It is indeed a great privilege to have this chance to add my contribution to the series of papers in her honor.

### BACKGROUND

I was born in Winnipeg, Manitoba. From a very early age, I was fascinated by living creatures. One day as I was walking to school, I saw a tiny bird, very close to me, in a hedge. My fifth-grade teacher happened to have a Peterson's field guide in the classroom, and I discovered that what I had seen had a name: it was a Golden-crowned Kinglet (*Regulus satrapa*). I was hooked for life.

My family moved frequently: from Winnipeg we moved to Saskatoon, Montreal, and finally to Vancouver, British Columbia, where I finished high school and then did my undergraduate work majoring in zoology at the Univ. of British Columbia. My honors thesis, done under the direction of M. D. F. Udvardy, was on niche differences between Chestnut-backed (*Poecile rufescens*) and Black-capped (*P. atricapilla*) chickadees and became my first published paper, in *The Wilson Bulletin* (Smith 1967a).

I stayed on at the Univ. of British Columbia to do a master's degree, working with Dennis Chitty on social behavior and survivorship in Black-capped Chickadees. This was my first color-banding project. Then I moved south of the border to do my Ph.D. at the Univ. of

Washington with Gordon Orians. I may have been his first graduate student not to work on blackbirds; my dissertation was on the development of prey recognition and impaling behavior in young Loggerhead Shrikes (*Lanius ludovicianus*).

During my graduate studies at the Univ. of Washington, I took a field course in Costa Rica through the Organization for Tropical Studies during the summer of 1969. This was my first experience in the tropics, and it was an extremely important influence on my perception of the natural world.

Immediately after completing and defending my dissertation, I began teaching at Wellesley College. There I started a field study on color-banded Black-capped Chickadees, for the first time focusing in particular on their winter dominance hierarchies. Four years later I got married, and my husband Gary Stiles and I moved to Costa Rica. There I worked hard to improve my Spanish, then taught biology (in Spanish), first at the Univ. of Costa Rica in San Jose, and later at the National Univ. in Heredia. During the four years I lived in Costa Rica, I did research on a color-banded population of Rufous-collared Sparrows (*Zonotrichia capensis*) on the Univ. of Costa Rica campus, as well as hand-rearing work with both Turquoise-browed Motmots (*Eumomota superciliosa*) and Great Kiskadees (*Pitangus sulphuratus*).

My marriage did not work out, and I returned north in 1977 to teach briefly at Adelphi Univ. before moving on to Mount Holyoke College, where I settled in 1979, and where I still am today.

### AREAS OF INTEREST

Most of my published work can be placed into one of three general topics, each of which is known to have interested Margaret Nice. The first two are strictly research: (1) the development of behavior, as addressed by hand-rearing studies; and (2) the social behavior of

<sup>1</sup> Dept. of Biological Sciences, Mount Holyoke College, South Hadley, MA 01075, USA; e-mail: ssmith@mtholyoke.edu

free-living birds, as addressed by color-banding studies. The third topic is more general and can be described as the importance of studying bird behavior without preconceived biases about the roles of males and females.

### ONTOGENY EXPERIMENTS

In her landmark study on behavioral development in Song Sparrows, Margaret Nice (1943) obtained extensive data not only on hand-reared birds, but also on young sparrows in the wild. I based the experimental design for my work with Loggerhead Shrikes on her example (Smith 1972, 1973a).

In the field, I checked eight shrike nests daily, looking at the behavior of both adults and nestlings. After the young had fledged, I followed two family groups (totaling 13 young birds) until the young dispersed naturally. I then hand reared more than 60 young shrikes, with the developmental data on free-living shrikes as a baseline for comparison.

*Ontogeny of impaling in shrikes.*—Shrikes of the genus *Lanius* are well known for impaling their prey, and I was particularly interested in how such behavior developed in young shrikes. As predatory passerines, shrikes lack talons to hold down their prey. Most predatory birds lacking talons are restricted to eating only prey small enough to be swallowed whole. However, impaling behavior serves the same function as talons, thus allowing shrikes to exploit larger prey. Here I use the term “impaling” broadly to include both the wedging of prey in forks of a branch, and the anchoring of prey on a sharp thorn.

Starting about 20 days after hatching, young shrikes began what I termed “dabbing” behavior, in which the birds would take food in their bills, turn, and touch the food to their perch. Approximately two days after the onset of dabbing, the birds began pulling the food along the perch toward their bodies; this I termed “dragging” behavior. Lorenz and von Saint Paul (1968) described very similar types of behavior in the development of impaling in three other *Lanius* species.

At first, dragging behavior was not directed toward suitable locations (thorns or forks). However, if such items were available, the birds gradually started directing their dragging more and more to appropriate places, until at

last they became proficient at impaling prey (Smith 1972).

I raised some shrikes in the absence of any impaling device, with only smooth dowels for perches. Shrikes kept in such conditions until they were  $\geq 75$  days posthatching, and then given thorns and forks, failed to use these for impaling, even if they had been given the daily opportunity to observe older shrikes impaling and wedging prey on thorns and forks in an adjacent cage. Thus the shrikes must have personal experience with suitable impaling locations in order for the dragging movements to develop into normal impaling behavior. Moreover, this experience must occur within a certain period (some time between 20 and 70 days after hatching), so the process involved in learning the orientation component of impaling seems very much like some form of imprinting.

*Factors directing predatory behavior in shrikes.*—Young shrikes, once fledged, are very curious and peck, pounce on, and even attempt to carry a wide variety of objects in their environment (Miller 1931a, 1937; Cade 1962, 1967; Smith 1973a). Under natural conditions, they begin catching small invertebrate prey within days of leaving the nest, and gradually become more skilled as they attempt to capture an ever wider variety of suitable prey. When hand reared, shrikes that were given a sequence of small to large live food to catch developed the ability to handle mouse-sized prey about 10 days sooner than birds not given such experience. Nevertheless, by the age of 40 days posthatching, all shrikes were capable of killing a mouse by directing pecks to the back of its neck in the manner of adult wild shrikes, even when this was the first live prey ever encountered (Smith 1973a).

I was curious to learn what aspects of a large (mouse-sized) potential prey object would be used by naïve shrikes to direct their pecks along its length. I presented my birds with a series of 12 wooden models, including some shown in Figure 1. The first model was plain, with no added cues, although I had divided it lengthwise into thirds, using very faint pencil marks. As expected, the birds ignored my pencil marks. They did, however, direct significantly more than two-thirds of their pecks to the two end thirds of this plain model. This makes sense, because terrestrial

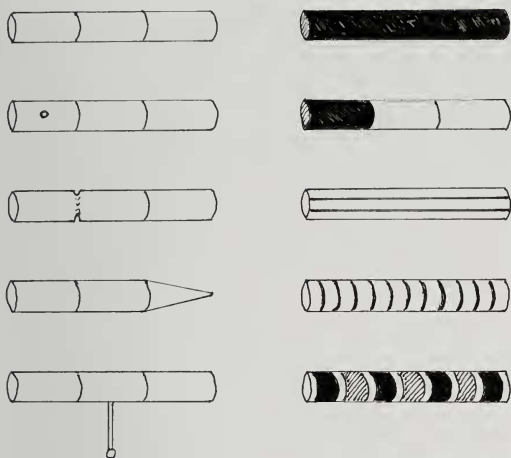


FIG. 1. Some sample models offered to hand-reared young birds. (Left) Unpainted models; from top: plain, eyespot, neck constriction, pointed tail, and plain moving model. Motion was achieved by inserting the nail into a slot in the floor of the cage. (Right) Painted models; from top: solid, end third, stripe pattern, ring pattern, and coral snake rings.

animals typically have their most vulnerable body parts near one end of their total body length.

The other 11 models all bore various cues singly or in combinations. These cues included eye spots, a "neck" indentation, and motion. When one of the end thirds differed from the other (by the addition of eye spots and/or neck), the birds all pecked significantly more at the different end. However, I found no evidence of heterogeneous summation; i.e., two or more of these cues did not elicit a consistently greater response than did just one of them. The shrikes may have been acting out of curiosity.

In contrast, motion, in and of itself, proved to be a powerfully directing cue. The shrikes gave a highly significant proportion of their pecks to the leading third of any moving model. A shrike would approach a moving model, follow it, then hop around to peck at the "head" end. As it would have been easier for the shrikes to follow a moving model and peck at the trailing end, this consistent strong response is clearly something other than just curiosity.

I also presented my shrikes with two mounted specimens of vertebrate prey: a Golden-crowned Kinglet and a deer mouse

(*Peromyscus maniculatus*). Rather to my surprise at the time, the shrikes paid virtually no attention to the stuffed bird. In contrast, their responses to the stuffed mouse were intense, much more so than to any other item I offered to them. When the mouse was in the normal upright position, all of the shrikes (regardless of prior experience) directed their pecks to the back of its neck. However, if in their approach they blew the cotton-stuffed mouse over onto its side or back, they directed their pecks instead to small extremities: feet, nose, or tail. This in itself I found fascinating; simply changing the orientation of an object can have a profound influence on the responses it elicits.

*Comparative studies.*—Over the next few years, I hand reared young birds of several species possessing differing types of diet: Black-capped Chickadees, Gray Catbirds (*Dumetella carolinensis*), Blue Jays (*Cyanocitta cristata*), House Sparrows (*Passer domesticus*), and two Neotropical species, Turquoise-browed Motmots and Great Kiskadees. The first of these studies was conducted on hand-reared chickadees, catbirds, and jays. To my surprise, all three of these, soon after fledging age, performed behavior that was indistinguishable from the dabbling behavior of young shrikes. This behavior was least common in catbirds, and involved no lateral components. In both chickadees and jays, it was more persistent, and later developed a lateral component as well. However, in both chickadees and jays this was pushing away from the body, in contrast with the pulling movements (dragging) in shrikes (Table 1). Both chickadees and jays hoard food; presumably these movements relate to storing behavior. It is more difficult to suggest a possible reason for the dabbling of young catbirds (Smith 1973b).

I presented these young birds with models similar to those used for shrikes (Fig. 1), but scaled appropriately for the size of the birds. All seven species, regardless of size or diet, aimed significantly more than 67% of their pecks to the two end thirds of their plain wooden model; this ranged from a low of 79.0% for the Gray Catbirds to a high of 93.6% for the Blue Jays (Smith 1974a, 1976a, 1978a, 1980a). When one of the end thirds of a model was provided with some additional cue, such as an eyespot or a "neck" constrict-

TABLE 1. Food manipulation in young passerines. Ages are days after hatching. Data from Smith (1973b, 1974a).

Species	Age at first dabbling	Age at first lateral movements	Type of lateral movements
Loggerhead Shrike	21	23	Pulling
Gray Catbird	12	—	—
Black-capped Chickadee	17	20	Pushing
Blue Jay	19	23	Pushing

tion (Fig. 1), all five of the species that received such models (chickadees, catbirds, jays, motmots, and kiskadees) directed the majority of their pecks at this different end. However, here again I found no consistent evidence for heterogeneous summation, so their responses may be explained simply by curiosity (Smith 1983).

An exception was the kiskadees' response to a model with one end sharpened into a "tail" (Fig. 1). Here the different third was the pointed end, but the kiskadees gave a highly significant response to the blunt end instead. Yet, it would seem to be easier for them to pick up the model by its point. Clearly, this response cannot be explained by curiosity; indeed, it suggests that kiskadees (which are known to eat lizards) may possess an innate recognition of "tail." Since many

lizards can shed their tails when caught, a kiskadee attacking the blunt end of such prey would be able to eat the whole thing, whereas those attacking the more pointed end might well end up with just part of a tail (Smith 1978a). It is unfortunate that I did not offer this "tail" model to any other predatory species.

Perhaps the most fascinating trend among the birds' behavior concerns their responses to motion. Figure 2 shows the responses of six species to plain moving models. The three predatory species (shrikes, motmots, and kiskadees) all responded by hopping around the moving model to direct their pecks at its leading third. Blue Jays gave virtually identical numbers of pecks at the front and hind end of this model. In contrast, the two nonpredatory species (as far as vertebrate prey is concerned) both gave a significant response to the trailing third of the model (Fig. 2).

*Responses to colors and patterns.*—Much of the work I did with colors and patterns was aimed at exploring mimicry systems through the behavior of potential predators. Most defensive mimicry systems (Batesian and Mullerian) function through predator learning (when a predator has a bad experience with a model) and predator generalization (when that predator generalizes to avoid attacking anything resembling that model; Wickler 1968, Morrell and Turner 1970).

However, the coral snake mimicry complex poses a different set of problems for would-be predators. True coral snakes have venom so lethal that any bad experience would result in death, and a dead predator cannot generalize to avoid anything at all. Given this problem, Wickler (1968) proposed that coral snakes are too lethal to serve as a model, and instead represent yet another type of defensive mimic, which he termed "Mertensian mim-

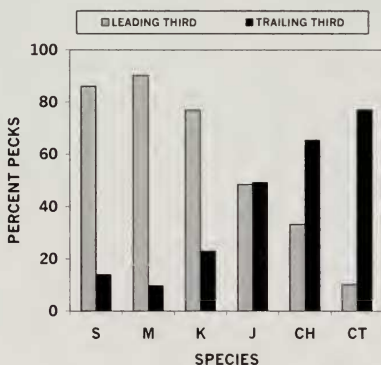


FIG. 2. Responses of six avian species to a plain moving model. The three predatory species, Loggerhead Shrike (S), Turquoise-browed Motmot (M), and Great Kiskadee (K) all responded significantly toward the leading third ("head") of the model. The omnivorous Blue Jay (J) pecked approximately the same at the leading and trailing thirds, while the two smaller species, Black-capped Chickadee (CH) and Gray Catbird (CT) pecked significantly more at the trailing third of the model.



FIG. 3. Nestling Turquoise-browed Motmots, with eyes tightly shut.

ics.” The actual models of this mimicry system then would be those snakes whose venom was sufficiently mild that a predator could survive being bitten, then proceed to avoid similar ring-patterned snakes. Certainly, Wickler said, there was no evidence that any predator could recognize coral snake patterns innately.

I decided to test this with Neotropical predators known to include small reptiles in their diet. The first species I used was the Turquoise-browed Motmot. This is a burrow-nesting species, and I obtained all of my nestlings before they had their eyes opened, so they had had no opportunity to see any colors or patterns other than what I gave them (Fig. 3).

I used four colors for the motmot experiments: yellow, red, light green, and dark blue, and presented these both as “solid” models, entirely covered with paint, and as “end-third” models, in which one end was painted, with the other two thirds being unpainted wood (Fig. 1). The motmots showed no hesitation in attacking solid models of each of these four colors, and directed most of their

pecks at the painted third of the end-third models.

Then I began my pattern experiments. The first patterned model I presented to the motmots was a “solid” one, the entire model being covered with wide yellow and narrow red rings (Fig. 1). The response was impressive; every bird flew up to the opposite corner of the cage, and in many cases gave alarm calls. No bird directed any pecks at this model at all. The next model I made also was red and yellow, with the same proportions of the two colors, but this time the model had wide yellow and narrow red stripes, running the length of the model (Fig. 1). This time the birds attacked with no hesitation. Finally, I made another ringed model, this time of wide light green and narrow dark blue rings. The motmots flew down and pecked this vigorously, directing their pecks particularly to the narrow dark blue rings.

When given end-third models with these patterns, the birds attacked all three, giving significant responses to the painted third of the red and yellow stripes and the blue and green

rings, but to the end farthest away from the red and yellow ringed pattern.

Clearly, therefore, the motmots were not afraid of a combination of red and yellow, since they attacked the striped model of those colors. Moreover, they were not afraid of a ring pattern itself, since they attacked the blue and green ringed model. However, when the rings were red and yellow, the birds showed a high degree of aversion. This I interpreted to be an innate response to a generalized coral snake pattern (Smith 1975).

My next experiments were on Great Kiskadees. These birds also have enclosed nests, so I could control the early experience of my birds with colors and patterns. Moreover, the geographical range of this species overlaps that of true coral snakes much more widely than does that of the motmots. This time I used five colors: red, yellow, black, dark green, and white.

The first pattern I had presented to the motmots was red and yellow rings, and so their negative response conceivably might have been due simply to novelty aversion (e.g., Coppinger 1970). Thus, after finding that the kiskadees readily attacked solid models of all five colors, the first pattern I gave them was wide white and narrow green rings. This they attacked with no hesitation. I could therefore conclude that neither novel patterns themselves, nor ring patterns in particular, were inherently frightening to these birds.

I gave two other ringed patterns to the kiskadees: red and yellow rings, and "coral snake" rings (wide red, narrow yellow, wide black, narrow yellow; see Fig. 1). No kiskadee approached either model. Nevertheless, the responses to the two differed; a few birds gave mild alarm calls to the former, while almost all of them gave high intensity alarm calls to the latter (Smith 1977).

Clearly, therefore, both of these potential predators have innate avoidance of patterns resembling coral snakes. Thus true, lethal, coral snakes can in fact serve as models in the mimicry complex, and the "Mertensian" mimicry hypothesis is unnecessary to explain the evolution and maintenance of this system.

Could this have been simply aversion to a generalized aposematic pattern? If so, then even birds that do not normally eat small reptiles, but often would encounter aposemati-

cally colored insects, might behave the same way. To test this, I hand reared Blue Jays and House Sparrows. I presented these birds with models painted a variety of color combinations: white and green rings; yellow and red rings; red and black rings; yellow and black "wasp" rings; black, white, and yellow rings in a monarch caterpillar pattern; and the red, yellow, and black coral snake ring pattern (Smith 1980a). The results were remarkable; all of the birds attacked every one of these models with no hesitation whatsoever (Fig. 4). Clearly, whatever made the kiskadees and motmots avoid red and yellow rings is not simply a universal aversion to warning coloration. Birds that normally do not encounter potentially lethal prey can afford to learn to avoid local aposematic patterns.

There are several lines of research one might follow based on some of this work. One involves a comparative approach. It would be interesting to choose a medium-sized omnivore that includes small reptiles in its diet. Perhaps there will be some populations that never encounter coral snakes, while other populations of this predator do overlap the coral snake range, either as residents or as migrants. One might predict that there would be a population difference in how hand-reared birds responded to coral snake patterns.

Coral snakes belong to the family Elapidae, and the diversity of this family in Australia is particularly high. At least some of the large Australian elapids have ringed patterns at an early age, which they lose later in life. Many Australian birds, such as some of the smaller kingfishers and perhaps members of the Cracticidae, are known to eat small reptiles. It would be interesting to see if such birds also had innate aversion to ringed patterns.

#### SOCIAL BEHAVIOR OF FREE-LIVING BIRDS

*Behavioral ecology of floaters: (1) sparrows.*—I first became interested in the behavior of floaters when I started color banding a population of Rufous-collared Sparrows on the Univ. of Costa Rica campus. This population had year-round breeding, and all the local suitable habitat was defended by resident, territorial pairs. To my temperate-trained eyes, the population was incredibly dense, although such densities are actually not at all uncom-



FIG. 4. Hand-reared young Blue Jay attacking a coral snake-ringed model.

mon in tropical regions (e.g., see Morton and Stutchbury 2000). Because of this high density, I had a lot of difficulty catching the sparrows. At first I tried mist nets. In no time I caught my first bird, and thought this would be easy. However, the territories were so small that the other birds could look down, see me putting up the nets, and then simply avoid them. It turned out the only way I was able to catch these birds was to set my nets before

dawn so that they could not see where I was putting them.

My initial goal was to band all of the territory owners. This was not easy; if another bird entered the net in a given (small) territory at first light, the resident sparrows would watch as I extracted it, and then would avoid the net for the rest of the morning. So, when I caught unmarked sparrows, banded them, and discovered they were not members of the

resident pairs, I was at first bitterly disappointed. They were just floaters—what a waste of bands, which were not easy to obtain in Costa Rica at that time. I was sure I would never see these birds again.

But I did see them. When the first of my resident birds vanished, only to be replaced with a bird I had banded, in that very same (tiny) territory over two months previously, I was amazed. When it happened again, I began to realize that the floaters in my population clearly did not lead the sort of random, wandering existence usually assumed to be typical of floaters. So, I decided to focus my study on the social behavior of these birds.

I found that floaters tended to enter breeding territories most frequently in very early morning, then spend much of the rest of the day in a block of woods adjacent to my campus population that was unsuitable for sparrow breeding territories. Moreover, the marked floaters did not range evenly over my entire study area; instead, they had stable and highly restricted home ranges, being made up of just some of the breeding territories in the area.

Male floaters had home ranges encompassing 3–5 breeding territories. Interestingly, these were not necessarily contiguous. In contrast, female home ranges typically consisted of just one single breeding territory. The floaters of each sex had a consistent, well-defined dominance hierarchy for each of the territories within their home range. When an adult territory owner died, it was quickly replaced by the dominant local floater of the appropriate sex (Smith 1978b).

Twenty-eight of the more than 50 floaters I banded during the next three years (15 females and 13 males) succeeded in becoming territory owners within my study area. Thirteen of the 15 females, and 6 of the 13 males had been banded in the territory they later came to own. Of the remainder, the two females were banded a mean of 50 m away from their first territory, and the seven males a mean of 65.7 m away (Table 2). Several of these were within 10 m of the block of woods mentioned above, and the rest may well have been moving between the woods and their home range when I caught them.

I estimated that approximately half of the sparrows on my study area were floaters, yet

TABLE 2. Successful underworld Rufous-collared Sparrows. Data from Smith (1978b).

Sex and individual	Minimum time in the underworld (months)	Distance (m) between place marked and first territory
Females		
KWR	0.5	0
RG	0.5	0
OY	1.0	0
RRO	1.0	40
WR/WR	1.0	0
YRB	1.0	0
BY	2.0	0
YY	2.0	0
GHL	2.5	0
GK/GK	3.0	0
RYK	3.5	0
YB	3.5	0
GG	5.0	0
RB/RB	5.0	60
OO	8.0	0
Males		
BYG	0.5	0
YR2	1.5	0
RBO	2.5	60
RY/RY	2.5	50
WO/WO	2.5	80
YR	2.5	0
KK	3.0	0
OWK	3.0	100
IBG	5.0	120
RG/RG	7.0	10
RGW	7.0	40
RBO2	8.0	0
YB/YB	12.0	0

a superficial glance at the area would detect primarily, and perhaps exclusively, the territory owners. I therefore termed these elusive floaters, with their highly organized social system, “the underworld” (Smith 1978b).

The only way for a young sparrow to obtain a breeding territory in suitable habitat, at least in my study area, was to join the underworld. Dispersing young birds that are still in striped juvenal plumage are more or less tolerated by adults, and can move about assessing where to set up their floater home ranges. Each bird presumably can assess the following four factors: territory quality, number of floaters of its sex already there, potential relations with its future mate, and health of the rival owner.

The relative importance of these four factors depends upon the gender of the floater. In my Costa Rican study area, Rufous-collared



Sparrows showed both year round breeding and year round female dominance. Perhaps as a result of this dominance, females can shift territories after having become an owner. Of my 10 records of owner territory shifts, only one was by a male; the other nine were by females. Probably most such shifts are to areas of higher quality.

This difference in dominance likely has strong effects on the relative importance of several of the four factors mentioned above. For males, who seldom shift territories after becoming owners, territory quality will be of very high importance; it is probably better for a young male to be relatively low ranked in the floater hierarchy of a high quality territory than to be more highly placed in a poorer quality territory. The relationship with future mates also is more important to males, since they are subordinate to females; this may explain the observed disjunct home ranges of male floaters.

For females, who can shift territories later more easily than males, starting rank likely is more important than territory quality, at least in fairly uniform habitat. Relations with future mates will be less important to females than to males, as resident males usually will not be able to reject them. Finally, health of the rival owner should be equally important to both male and female floaters (Smith 1978b).

There are several follow up studies I would love to see done. One interesting project on Rufous-collared Sparrows might be to work in an area of year round breeding, but with very marked variation in habitat quality. Under such circumstances there should be some territories with relatively large numbers of male floaters, while others might have few or even none (one would predict that female floaters would be more evenly distributed here). With the current technology allowing radio tracking of birds, determining floater home ranges and hierarchies should be considerably easier than it was when I first tackled it in the 1970s. Knowing where the floater hierarchies are longest might provide a "bird's eye view," as it were, for relative territory quality. One could compare male floater density with other factors more commonly used to estimate territory quality, such as availability of suitable nest sites, food, cover, or the like, to see which factors correlate most strongly with the birds'

own choices. One also might predict that there could be certain lower quality territories where no male floaters occurred at all. It would be interesting to perform removal experiments on such territories to see if and from where any replacements came. If territories existed with no female floaters, those indeed would be inferior quality real estate.

Another interesting project would be to look at the social organization of underworld Rufous-collared Sparrows in more strongly seasonal, south temperate locations. Would the floaters there have such a highly organized system? When would this system form, and how long would it last?

*Behavioral ecology of floaters: (2) chickadees.*—When I arrived at Mount Holyoke College in the fall of 1979 and began color banding Black-capped Chickadees, I once again encountered floaters and, like the underworld sparrows, they also had restricted home ranges and well-defined dominance hierarchies. Floaters during the breeding season are well known; these are the birds capable of breeding but prevented from doing so by the behavior of others (Hensley and Cope 1951, Stewart and Aldrich 1951, Brown 1969, Smith 1978b). However, my chickadee study was conducted mostly during winter on nonbreeding flocks, and I was quite unprepared to find floaters at that time of year. There were indeed winter floaters, and in quite large numbers, too.

Most winter chickadees in my study area belong to a single home flock. These birds, which I termed "flock regulars," are organized into linear dominance hierarchies. The flocks, when first formed, contain equal numbers of males and females. Because the top-ranked male turns out to be paired with the top-ranked female, and so on down through the hierarchy, I suggested that a 10-bird flock (for example) actually functions as a hierarchy of five pairs (Smith 1988a, 1991).

Chickadee winter floaters have home ranges that include from 3–6 flock ranges. They typically move very rapidly between flocks; hence the term "flock switcher" (Smith 1984). I have found no gender-based difference in home range size of these birds.

Floaters initially ranked at the bottom of each of their flock hierarchies, below all regular members of their sex. However, given the opportunity, these birds could settle into one

of their flocks and assume a much higher rank. This was true for both male and female floaters. Such insertions always occurred after one of the regular members of a flock had vanished. Generally, only high-ranked openings were filled in this way; lower-ranked slots remained empty.

I observed two different kinds of floater insertion. In simple substitution, a high-ranked bird vanishes and is replaced by the highest ranked floater of the same sex, which pairs with the mate of the vanished bird; the ranks and pair bonds of the other members of the flock remain unchanged. Complex substitution involves two pairs within the flock. Here, if a member of the alpha pair disappears, two birds attempt to replace it: the top-ranked winter floater and a member of the beta pair. The latter succeeds in moving up, and the floater then inserts at the beta position (Smith 1984).

Floaters attempt to insert into only high-ranked slots in a flock; low-ranked slots stay unfilled all winter. Significantly, in most years only the top few pairs succeed in gaining local breeding territories; the lower ranked pairs typically are driven away at flock break up in the spring.

Having observed how this system worked under natural conditions, the next step was to conduct removal experiments. As I also was interested in long term survivorship in my study population, I obtained funding to build an aviary. Thus, when I removed a bird from its flock I could hold it in my aviary, observe the replacement process, then return the bird back into its flock and describe the subsequent social interactions (Smith 1987).

From November 1984 to January 1986, I performed 10 removal experiments. I decided to proceed under several restrictions. First, I removed birds only between November and February of any year to be sure that the flocks had fully formed in the fall and had not begun to break up in the spring. Birds were removed only from completely banded flocks. I removed each of the birds in the morning, to give it plenty of time to settle and discover food and roosting sites in the aviary well before nightfall. Finally, I took birds only when the weather was relatively warm, because they were held singly in the aviaries (Smith 1987).

Of the 10 birds removed, six (three females and three males) rapidly were replaced by

TABLE 3. Removal experiments on Black-capped Chickadees. Data from Smith (1987).

Removed bird	Flock size	Replaced?	Time (h) until first observed supplanting
#1 female	8	Yes	26
#1 female	4	Yes	5.5
#2 female	6	Yes	27
#1 male	4	Yes	30.25
#1 male	8	Yes	22
#2 male	4	No	
#3 male	6	No	
#3 male	6	No	
#4 male	8	No	

floaters. All six of these birds were highly ranked in their flocks (Table 3). The other four birds (all males) were not replaced; all four of these were the lowest ranked birds of their sex in their flocks.

For all six high-ranked slots that I created in this way, the floater response was extremely rapid. One of the six insertions was by complex substitution, the other five by simple substitution. All six substitutions involved rapid and radical changes in dominance relations; settling birds began supplanting birds that, just hours before, had ranked well above them. Yet these major jumps in rank occurred literally overnight; the mean time between removal and first supplanting of the closest rival by the inserting floater was just 22.3 h. By the end of the second day, all the new ranks were firmly established.

No floater attempted to settle into any of the slots made by removing the four low-ranked males. This supports the field observations that low-ranked openings remain unfilled all winter.

I kept each of the captive birds in the aviary for four days, after which I released them back into their respective flocks. Upon release, all 10 birds regained their former rank immediately. They re-associated closely with their former mates, and lost no time in chasing away the floater that had briefly replaced them. The six floaters that had inserted then temporarily restricted their home range such as to avoid the flocks they had joined. Two of these six floaters later inserted into genuine openings and became local breeders the following spring (Smith 1987).

It turns out that I was fortunate to do these

removal experiments when I did them; soon afterward, the overall numbers of winter floaters in my study area dropped considerably, and thereafter, some high-ranked openings have remained unfilled, at least in certain years (Smith 1990). Nevertheless, I continue to have winter floaters in my study area, and have had at least some successful insertions (both simple and complex substitutions) in virtually every year so far.

Precisely what occurred to cause the marked drop in floater density in my study area is unclear. However, at approximately the same time, Tufted Titmouse (*Baeolophus bicolor*) numbers increased strongly in my study area. Whether or not the increased competition from this larger parid species had an impact on chickadee floater density is unknown.

Summer floaters (i.e., those during the breeding season) also occur in my chickadee population (Smith 1989, 1991). Perhaps the most interesting thing about these birds is that during 23 years of study every one I have seen so far has been present in the study area the previous winter. The vast majority (98%) of these birds were low-ranked regular members of a study area winter flock; the rest were winter floaters. Among chickadee summer floaters, male and female behavior usually is quite different. Male summer floaters are relatively easy to find; they often are quite vocal, concentrating their time in the less heavily used portions of local breeding territories. Female summer floaters are far more difficult to detect; they tend to be much more silent and skulking.

Whether or not territory owners will tolerate the presence of summer floaters probably depends upon local conditions that year. In my study area, summer floaters have occurred in only some years, and apparently are completely absent in others. When present, both male and female floaters can insert and replace a breeder of their sex; the absence of summer floaters in certain years is confirmed by the lack of replacements of breeders that vanish in May or June (Smith 1989).

*Other aspects of population ecology and social behavior of chickadees.*—My first field research project was on differences in foraging locations used by Black-capped and Chestnut-backed chickadees near the Univ. of British Columbia in Vancouver. I found that

Chestnut-backed Chickadees foraged more in conifers, while Black-capped Chickadees foraged approximately the same amount in deciduous and in coniferous trees. There were height differences as well, with Chestnut-backed Chickadees feeding, on average, higher than Black-capped Chickadees. However this difference primarily reflected the fact that local conifers were much higher than deciduous trees; the mean distance from the top of the tree for each species was essentially the same (Smith 1967a). Most of my data were taken from mixed flocks, with records taken of both species each session. Looking at these paired records, one can see that the niche differences showed up consistently. Thus, the weather effects, later so well documented for parid foraging by Grubb (1975, 1977), probably did not have a major effect on my results.

My first color-banding study of Black-capped Chickadees also was conducted in Vancouver, British Columbia. There I looked primarily at changes in social behavior over time, and found that increased aggression associated with flock break up in the spring was correlated, in both years of the study, with a marked drop in overall chickadee density; all chickadees surviving this spring period obtained local breeding territories. I therefore concluded that the local breeding density of chickadees was regulated by territorial behavior (Smith 1967b).

The second location where I worked with color-banded chickadees was on the campus of Wellesley College in eastern Massachusetts. I was particularly interested to learn whether dominance hierarchies generated at feeders differed from those operating away from feeders. Although at the time I was disappointed that I detected no differences, I became grateful, as feeder-generated interactions tend to be more easily observed. I also hypothesized that in flocks containing more than one old (i.e., former breeder) male, the relative dominance between these birds might be affected by location. I thought that perhaps when a flock was near the nest site of one male, he would be dominant, but that this might shift when the flock entered the former breeding territory of the other male. Again my hypothesis was wrong; I found that my dominance hierarchies remained constant throughout each flock's entire home range (Smith

1976b). This study, which lasted four years, did support my third hypothesis, that alpha pairs would obtain better quality territories than would lower-ranked pairs. The alpha pairs' territories tended to be smaller in area, but with greater overall cover; they also had higher overall nestling feeding rates than did territories of lower-ranked pairs (Smith 1976b).

The rest of my work on chickadees involves my third population, in western Massachusetts. This ongoing study already has continued for more than twenty years.

As mentioned above, each Black-capped Chickadee winter flock is actually made up of a set of component pairs. I found, using the method of Ficken et al. (1981), that even members of pairs made up of two juvenile birds associated more closely with each other than with other members of their flock, and that this close association can be discerned in the fall, as well as later in the year (Smith 1990).

Pair bonds can persist for many years in chickadees (Odum 1942, Glase 1973, Smith 1991). However, they are not necessarily fixed for life. Thus, even when both members of a former pair are alive, one member can, under certain circumstances, desert the other and find a new mate. The first time I encountered this behavior was in my Wellesley population. An alpha male had a nest in an exposed metal pipe in a parking lot for at least two years in succession. The pipe would become very hot in the sun, and during incubation, his mate often could be seen panting at the nest entrance (in Black-capped Chickadees, females do all the incubation). The male had a different mate each year; even though both females survived the summer, they each joined another flock the following fall (Smith 1974b).

Divorce (the breaking of a former pair bond, where both members of the pair are still alive) can be initiated by both males and females. Although the Wellesley examples mentioned above appear to be a mode of escape from a difficult situation, most of my records can be thought of as a sort of social climbing. In 10 years of data from my current study population, there were 15 cases of divorce, while 79 other intact pairs (just over 84%) stayed together. Of the 15 divorces, 10 were initiated by females, and five by males. All 15

occurred after the death of another chickadee. Although these occurred both in the breeding and the nonbreeding season, I will treat the resulting changes in terms of the subsequent rank in the nonbreeding flocks. Fourteen of the records involved clear increases in rank. Each male initiator went from beta to alpha rank. Eight of the ten female initiators went from second- to top-ranked position, and one went from third-ranked to second-ranked position. The final record was slightly different; here a female that was top-ranked in a four-bird flock moved to become the top-ranked female in an eight-bird flock (Smith 1992).

In winter flocks, males rank higher than females. However, this gender-based dominance difference has no significant effect on overwinter survival; females survive the winter just as well as do males. Nevertheless, rank does have a significant effect on winter survival, but it is within-sex rank that matters, not between-sex rank. Thus, both members of a flock's high-ranked pairs survive significantly better than do members of lower-ranked pairs (Smith 1991, 1994).

Remarkably, at least in the first 10 years of my study, I found that significantly more young birds settled into my study flocks during falls preceding high winter survival, than in falls preceding lower winter survival (Fig. 5), suggesting that at some level chickadees during late summer or early fall, when the nonbreeding flocks are forming, can somehow assess conditions in the coming winter (Smith 1994). As yet I have not determined whether it is the older birds that assess the conditions and then regulate how many young birds to tolerate in the flocks as they form, and/or whether the young birds can detect these conditions and behave accordingly. Given the fact that many very different conditions could affect winter survival [food levels, involving both seed crops and possibly animal food as estimated (perhaps) by caterpillar damage on leaves; density and kind of predators and of their alternate prey species, to list just a few], this is not an easy question to resolve.

I have said that on average, females survive the winter just as well as do males. Nevertheless, male long term survivorship is somewhat higher than that of females (Smith 1994, 1995). The main time when the two curves diverge is when the birds are just over one

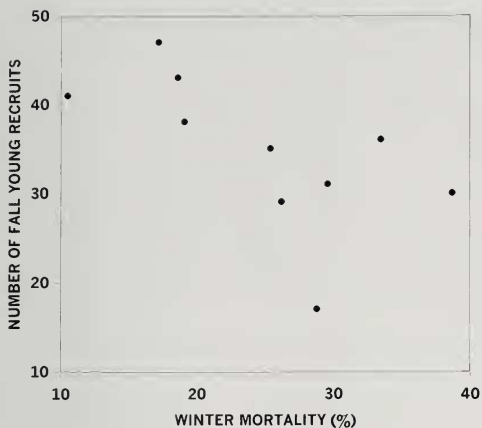


FIG. 5. Relationship between number of young Black-capped Chickadees settling into the nonbreeding flocks in the fall, and subsequent winter mortality in the study area. Significantly more young chickadees settled into the area before winters of low winter mortality; fewer settled before winters of higher mortality. From Smith (1994).

year old, the end (for most of them) of their first breeding season and first postbreeding molt (Fig. 6). Males typically survive this period very well, but many females vanish at this time. I tried to see how those females who survived this period differed from those that did not. I found two factors that were significantly related to yearling female survival in late summer and early fall. One was previous winter rank; those with high initial rank survived their first full summer significantly better than those with lower initial rank in the previous winter flocks.

The second factor concerned the females' mates. Young females paired with older, experienced males survived the late summer period better than did young females paired with inexperienced males; this effect was particularly pronounced in years when the nighttime temperatures during incubation were relatively low. Inexperienced males in other species have been shown to be relatively inefficient in levels of courtship feeding (Lifjeld and Slagsvold 1986); this also may occur in chickadees. I concluded that young females given relatively little food support during incubation, especially in particularly cold years, may incur sufficient energy drain that they cannot easily survive the subsequent costs of parental care and complete molt (Smith 1995).

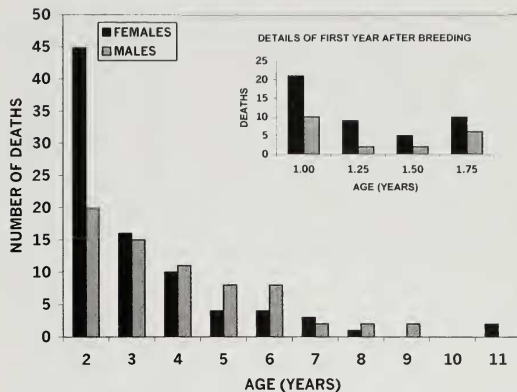


FIG. 6. Mortality of male and female Black-capped Chickadee breeders, starting with their second year of life (i.e., the first year after becoming breeders). Insert presents details of this critical year, separated into quarters: the first quarter ends on 30 June, the second 30 September, the third 31 December, and the fourth 31 March. Most of the difference between male and female mortality occurred during the first two quarters. Female mortality to the end of September (1.25 years) was significantly greater than male mortality during the same period. From Smith (1995).

## THE IMPORTANCE OF FEMALE-BASED QUESTIONS IN BIOLOGY

It was my population of Rufous-collared Sparrows, with its year-round breeding, that gave me my first experience with a social system in which females consistently dominated males. When I moved north from Costa Rica, I began searching through the literature and discovered that breeding female dominance was, in fact, a widespread phenomenon among monogamous birds, although often the reports of it were placed near the end of papers, and began with words such as "Oddly . . ." In combing through the literature, I came across a paper by Margaret Morse Nice (1949) titled "The question of sexual dominance." She had found that in Song Sparrows, females were dominant over males during the breeding season, and had speculated about how widespread this pattern might be. I therefore dedicated my paper on this general pattern in monogamous birds to her (Smith 1980b).

In that paper I brought together reports of breeding female dominance in 37 species from 18 avian families (Table 4). In many of these, males are dominant during the nonbreeding season; here dominance reversal must occur twice a year. I related this reversal

TABLE 4. Monogamous birds with breeding female dominance. Data from Smith (1980a).

Species	Family	Reference	Reversal?
<i>Sula leucogaster</i>	Sulidae	Simmons 1970	No
<i>Accipiter striatus</i>	Accipitridae	Reynolds 1972	No
<i>Falco rusticolus</i>	Falconidae	Cade 1960	No
<i>F. peregrinus</i>	Falconidae	Cade 1960	No
<i>Picoides pubescens</i>	Picidae	Kilham 1974	Yes
<i>Dendrocincla fuliginosa</i>	Dendrocolaptidae	Willis 1972	No
<i>Gymnophis bicolor</i>	Thamnophilidae	Willis 1967	Yes
<i>Garrulus glandarius</i>	Corvidae	Goodwin 1951	Yes
<i>Parus major</i>	Paridae	Hinde 1952	Yes
<i>Sitta carolinensis</i>	Sittidae	Kilham 1971	Yes
<i>S. canadensis</i>	Sittidae	Kilham 1975	Yes
<i>Sialia sialis</i>	Turdidae	Krieg 1971	Yes
<i>Muscicapa striata</i>	Muscicapidae	Davies 1977	?
<i>Lanius ludovicianus</i>	Laniidae	Miller 1931a	?
<i>Vireo solitarius</i>	Vireonidae	James 1978	?
<i>V. flavifrons</i>	Vireonidae	James 1978	?
<i>Setophaga ruticilla</i>	Parulidae	Ficken 1963	Yes
<i>Icterus galbula</i>	Icteridae	Miller 1931b	Yes
<i>Emberiza calandra</i>	Emberizidae	Andrew 1957	Yes
<i>E. citrinella</i>	Emberizidae	Andrew 1957	Yes
<i>E. schoenictus</i>	Emberizidae	Andrew 1957	Yes
<i>Melospiza melodia</i>	Emberizidae	Nice 1943	Yes
<i>Zonotrichia capensis</i>	Emberizidae	Smith 1978b	?
<i>Carduelis carduelis</i>	Carduelidae	Hinde 1956	Yes
<i>C. tristis</i>	Carduelidae	Coutlee 1967	Yes
<i>C. lawrencei</i>	Carduelidae	Linsdale 1957	Yes
<i>C. psaltria</i>	Carduelidae	Linsdale 1957	Yes
<i>C. flammea</i>	Carduelidae	Dilger 1960	Yes
<i>Carpodacus purpureus</i>	Carduelidae	Thompson 1960	No
<i>C. cassinii</i>	Carduelidae	Samson 1977	No
<i>C. mexicanus</i>	Carduelidae	Thompson 1960	No
<i>Loxia curvirostris</i>	Carduelidae	Tordoff 1954	Yes
<i>Pyrrhula pyrrhula</i>	Carduelidae	Hinde 1956	Yes
<i>Chloris chloris</i>	Carduelidae	Hinde 1956	Yes
<i>Coccothraustes coccothraustes</i>	Carduelidae	Hinde 1956	Yes
<i>Fringilla montifringilla</i>	Fringillidae	Hinde 1956	Yes
<i>F. coelebs</i>	Fringillidae	Marler 1956	Yes

to the relative costs to the two sexes in different seasons of the year. For males, high rank in the nonbreeding season can be of extreme importance, as it may affect the quality of breeding territory that can be obtained in the spring. Those having the poorest rank may not get a territory at all and, since males in many species outnumber females, only males with the best territories are ensured of acquiring mates. Low winter rank to a female will have little direct effect on her breeding success the following spring, but to a male, it may prevent him from breeding at all. Thus, in the nonbreeding season, the advantages of dominance to a male will be greater than the

disadvantages of subordination to the female. However, during the breeding season the reverse is true. The enormous costs of egg production (often entirely overlooked in papers assessing costs of parental care) makes the early breeding season a period of critical importance to females. If dominance permits a female to obtain more food during this period, it could give her a clear advantage over more subordinate females. At the same time, resident males, who have succeeded in obtaining a territory and a mate, actually may benefit from their mate's dominance if it results in higher quality of their offspring. Thus, during the breeding season, the advantages of domi-

nance to a female are greater than the disadvantages of subordination to the male (Smith 1980b).

In my Rufous-collared Sparrow population in Costa Rica, only one class of birds could supplant adult females: the dependent juveniles. This observation got me thinking about the kinds of behavior so often referred to as “begging” in birds. Begging occurs in two common situations: by the female during courtship feeding and by dependent fledglings in family flocks. However, courtship feeding happens at the peak of female dominance, and the literature contains many reports of dependent fledglings, such as my sparrows, being dominant over adults (e.g., Marler 1956; Willis 1967, 1968). The word “begging” contains a lot of unspoken implications that, on careful examination, are not supported by facts. Indeed, the birds doing the so-called “begging” typically are dominant over the birds that respond by giving them food. I therefore proposed that it would be more accurate to term this kind of activity “demand behavior” (Smith 1980c).

The interpretation of the rapid wing movements variously called “fluttering” or “quivering” often seems to be based on unspoken assumptions. Perhaps because it often is given by females in sexual contexts, it has frequently been termed “appeasement displays” (e.g., Hardy 1961, Zahavi 1971), even when applied to females in the early breeding season, the time when their dominance over males typically is most pronounced. I suspect this illustrates circular reasoning: females do this, so it must be appeasement, and since females are doing this appeasement behavior, they must be subordinate. I suspect that most wing fluttering behavior may be a kind of threat display, perhaps being elicited in situations of strong conflict of opposing drives, as shown by Jones (1968) for Great Tits (*Parus major*). Certainly rapid fluttering wing movements in both captive and free-living Loggerhead Shrikes are anything but appeasement; rather, they are highly aggressive in nature (Smith 1973c).

Breeding female dominance, being such a widespread pattern in monogamous birds, also may be a factor in the so-called “reverse” size dimorphism found in raptors. In species such as chickadees or Song Sparrows, interactions involved in dominance reversal will not be

particularly dangerous. In contrast, raptors, with their talons and powerful hooked bills, have the ability to inflict real damage. Female raptors’ much bigger size may ensure their dominance without the necessity of establishing dominance through agonistic encounters. It is interesting here that the accipiters, which eat primarily birds, show perhaps the most pronounced size dimorphism among avian raptors (Smith 1982).

Not long ago I read one too many papers based on two unstated, unexamined assumptions concerning female behavior (or the lack thereof). Many suggest or state outright that the vast majority of extrapair copulations (EPCs) are the result of the resident male’s failure to drive off male intruders. One unstated assumption here is that females never move beyond the boundaries of their home territory. Another is that females will mate unquestioningly and unselectively with any male that approaches her. I found both of these assumptions decidedly hard to believe.

I decided to test these assumptions with Black-capped Chickadees. I used field notes from my two previous color-banding studies to add to my current observations, and accumulated 13 records of EPCs in which all three birds (the female, her mate, and the other male) were color banded and their winter ranks known.

In all 13 of the EPCs, the “other” male had ranked above the female’s own mate during the past winter (Table 5). Furthermore, in nine cases, the EPCs occurred in the territory of the other male. Thus, females were being highly selective of their EPC partners, and typically left their own territories in active search of superior chickadees (Smith 1988b). More recently, DNA fingerprinting studies have supported the idea that female chickadees prefer high-ranked males as EPC partners (Otter et al. 1994, 1998, 1999). The pattern of females leaving their own territory to approach better quality partners is now known to be quite common, as shown by the work of Stutchbury and her colleagues on Hooded Warblers (*Wilsonia citrina*; Stutchbury et al. 1994, 1997; Neudorf et al. 1997; Tarof et al. 1998; see also Morton et al. 2000, Kempenaers et al. 1992, and Westneat et al. 1990).

A number of papers (see Smith 1988b) have suggested that male floaters might “sneak

TABLE 5. Extrapair copulations in Black-capped Chickadees. Data from Smith (1988b).

Year	Place <sup>a</sup>	Rank of mate	Rank of other male	Location of EPC
1963	BC	2	1	Other male
1963	BC	2	1	Other male
1963	BC	2	1	Other male
1963	BC	2	1	Own male
1964	BC	2	1	Other male
1964	BC	2	1	Other male
1964	BC	2	1	Own male
1971	E.MA	3	1	Other male
1982	W.MA	2	1	Own male
1982	W.MA	3	2	Other male
1984	W.MA	2	1	Own male
1985	W.MA	3	1	Other male
1986	W.MA	2	1	Other male

<sup>a</sup> BC = British Columbia (Vancouver), E.MA = eastern Massachusetts (Wellesley), W.MA = western Massachusetts (South Hadley).

EPCs" with resident females. This strikes me as extremely unlikely. Breeding females typically are dominant over males (Smith 1980b), and thus in most species could reject any unwanted approaches. Breeding season floaters usually are birds that have lost in competition for breeding territories, so presumably the female's own mate is both higher-ranked and more fit than any floater. Thus, the chances of any resident female permitting EPCs with male floaters seem to be very slim indeed. On the other hand, female floaters just might engage in EPCs with resident males. Gowaty and Karlin (1984) have found multiple maternity in Eastern Bluebirds (*Sialia sialis*); it is conceivable that female floaters might mate with local territorial males, then attempt to "dump" the resulting egg(s) in nests nearby. Careful field work combined with DNA fingerprinting techniques might find this to be a not uncommon pattern.

Margaret Morse Nice's autobiography is titled "Research is a passion with me" (Speirs 1979), and so it is for me. My studies have led me to unexpected turns and twists in roads I had thought to be straight and direct; avian research has been, and continues to be, my great delight. Margaret Morse Nice has set a shining example, and I am honored to be following in her footsteps.

#### ACKNOWLEDGMENTS

For early inspiration, many thanks to Ian McTaggart Cowan, who first told me it was possible to make a

career in ornithology, and to J. Mary Taylor, whose arrival at U.B.C. showed me for the first time that it was possible for a woman to be a professor of zoology. For financial support, my thanks to Sigma Xi and to the National Science Foundation. For intellectual stimulation along the way, my thanks to Jim Bendel, Denis Chitty, Muriel Harris, Margaret Lewis, Mary Taylor, Gordon Orians, Dennis Paulson, Geraldine Gauthier, Helen Padykula, Christopher Perrins, Laurene Ratcliffe, John Kricher, Ted Davis, Don Kroodsma, and Doris Atkinson, among many others.

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